



ELSEVIER

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

SCIENCE @ DIRECT®

Deep-Sea Research I 50 (2003) 1537–1549

DEEP-SEA RESEARCH  
PART I

[www.elsevier.com/locate/dsr](http://www.elsevier.com/locate/dsr)

# The beam attenuation to chlorophyll ratio: an optical index of phytoplankton physiology in the surface ocean?

Michael J. Behrenfeld<sup>a,\*</sup>, Emmanuel Boss<sup>b</sup>

<sup>a</sup> National Aeronautics and Space Administration, Goddard Space Flight Center, Code 971, Building 22, Greenbelt, MD 20771, USA

<sup>b</sup> School of Marine Sciences, 209 Libby Hall, University of Maine, Orono, ME 04469-5741, USA

Received 27 February 2003; received in revised form 13 August 2003; accepted 4 September 2003

## Abstract

The particulate beam attenuation coefficient ( $c_p$ ) is proportional to the concentration of suspended particles in a size domain overlapping that of the phytoplankton assemblage.  $c_p$  is largely insensitive to changes in intracellular chlorophyll concentration, which varies with growth irradiance (a process termed ‘photoacclimation’). Earlier studies have shown that the ratio of  $c_p$ :chlorophyll (i.e.,  $c_p^*$ ) exhibits depth-dependent changes that are consistent with photoacclimation. Similar relationships may likewise be expected in the horizontal and temporal dimensions, reflecting changes in mixing depth, incident irradiance, and light attenuation. A link between  $c_p^*$  and more robust photoadaptive variables has never been explicitly tested in the field. Here we use five historical field data sets to directly compare spatial and temporal variability in  $c_p^*$  with two independent indices of photoacclimation: the light-saturated, chlorophyll-normalized photosynthetic rate,  $P_{opt}^b$ , and the light-saturation index,  $E_k$ . For the variety of oceanographic conditions considered, a first-order correlation emerged between  $c_p^*$  and  $P_{opt}^b$  or  $E_k$ . These simple empirical results suggest that a relationship exists between a bio-optical variable that can potentially be retrieved remotely ( $c_p^*$ ) and physiological variables crucial for estimating primary productivity in the sea.

© 2003 Elsevier Ltd. All rights reserved.

**Keywords:** Beam Attenuation; Phytoplankton; Photosynthesis

## 1. Introduction

The particulate backscattering coefficient ( $b_{bp}$ ), chlorophyll concentration (Chl), beam attenuation coefficient ( $c$ ), particulate organic carbon (POC) concentration, and net primary production (NPP) are central variables of contemporary oceanographic research that share an important characteristic: they all vary to first-order with the

suspended particle load. Oceanic particle assemblages include detrital components of in situ or terrigenous origin, viruses, bacteria, phytoplankton, zooplankton, and inorganic compounds. Together, these constituents create continuous and relatively conserved particle size distributions, with Junge-like differential slopes of  $\sim 4$  (e.g., Bader, 1970; Stramski and Kiefer, 1991). Deviations from this ‘typical’ size spectrum can be pronounced, though, such as in coastal waters and during bloom events.

The various measures related to particle concentration ( $b_{bp}$ , Chl,  $c$ , POC, NPP) are dominated by different components and size domains of the assemblage.

\*Corresponding author. Tel.: +1-301-286-2742; fax: +1-301-286-5337.

E-mail address: [mjb@neptune.gsfc.nasa.gov](mailto:mjb@neptune.gsfc.nasa.gov) (M.J. Behrenfeld).

#### 4. Discussion

The apparent consistency between spatio-temporal changes in  $c_p^*$  and our two indices of photoacclimation is intriguing, given the many dissimilarities in these variables. For example, while  $c_p$  is sensitive to all particles in the water, its variability is largely determined by particles in

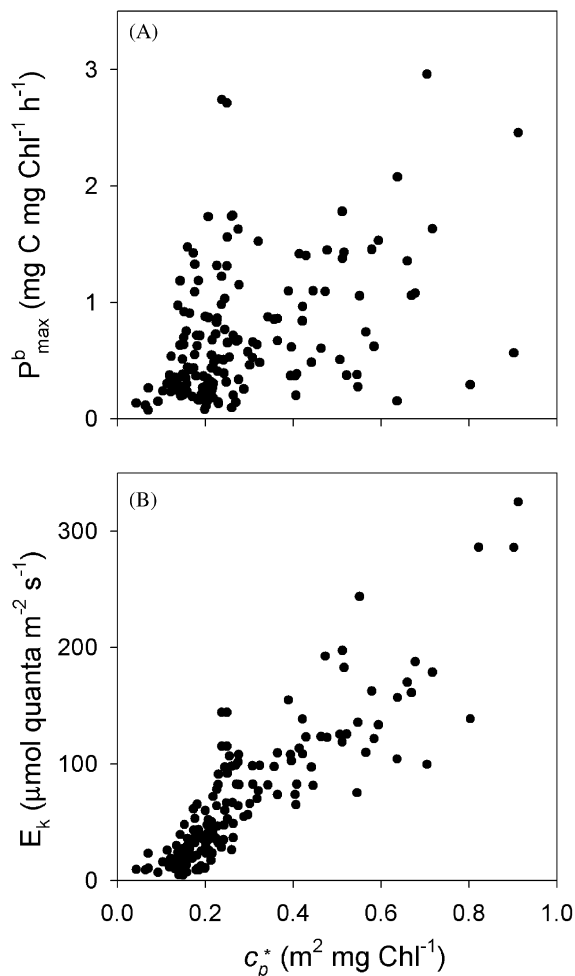


Fig. 5. The chlorophyll-normalized particulate attenuation coefficient ( $c_p^*$ ) versus (A) light-saturated photosynthesis ( $P_{\max}^b$ ) ( $r^2 = 0.23$ ;  $n = 161$ ) and (B) the light saturation index,  $E_k (= P_{\max}^b / \alpha^b)$  ( $r^2 = 0.76$ ;  $n = 161$ ) for the OliPac study. The highest value for  $P_{\max}^b$  has been omitted from (A) to better view the remaining data. The omitted variable pair is  $P_{\max}^b = 4.54 \text{ mg C (m}^3 \text{ h)}^{-1}$  and  $c_p^* = 0.82 \text{ m}^{-1}$ .

$\sim 0.5$  and  $20 \mu\text{m}$  range (whether bacterial, detrital, or algal) for typical open ocean particle size distributions (Morel, 1973; Stramski and Kiefer,

1991; Boss et al. 2001). Consequently, even in the open ocean only a fraction (but often dominant) of  $c_p$  (or POC) can be attributed to phytoplankton (Letelier et al., 1996; DuRand et al., 2001; Gundersen et al., 2001; and see discussion in Fennel and Boss, 2003). In fact,  $c_p$  is not even equally influenced by the different  $< 20 \mu\text{m}$  algal groups, with ultraplankton ( $1\text{--}2 \mu\text{m}$ ) and nanoplankton ( $2\text{--}20 \mu\text{m}$ , but particularly  $2\text{--}3 \mu\text{m}$ ) apparently having a greater influence on  $c_p$  than the picoplankton, *Prochlorococcus* and *Synechococcus* (DuRand and Olson, 1996). In addition, variability in  $c_p^*$  can arise from a change in the phytoplankton size distribution simply because normalization to chlorophyll involves the division of one size domain ( $c_p \sim 0.5\text{--}20 \mu\text{m}$ ) by another ( $\text{Chl} > \text{filter pore size}$ ). Photosynthetic rates, on the other hand, are influenced (in a growth-rate dependent manner) by all taxonomic groups of algae collected on a filter and the derived photoacclimation variables reflect physiological changes in the phytoplankton fraction alone. These issues, among others (e.g., changes in  $c_c^*$ , influence of coccoliths (Balch et al., 2001)), compromise any potential for relating  $c_p^*$  to photoacclimation, particularly over large horizontal and temporal scales. It was somewhat surprising, therefore, that our empirical analysis did reveal a first-order correspondence between  $c_p^*$  and  $P_{\text{opt}}^b$  (Fig. 6) or  $E_k$  (Fig. 5B). One interpretation of this result is that  $c_p^*$ ,  $E_k$ , and  $P_{\text{opt}}^b$  are not causally linked, but simply covary under certain environmental conditions. An alternative interpretation, and the one we favor, is that the dynamic range of variability in cellular chlorophyll resulting from physiological responses to changing light and nutrient conditions is sufficient to overcome the formerly identified dissimilarities between  $c_p$  and phytoplankton carbon biomass.

The photosynthesis–irradiance relationship can exhibit a tremendous degree of flexibility, with two primary types of change: ‘ $E_k$ -dependent’ and ‘ $E_k$ -independent’ (Behrenfeld et al., 2003). Photoacclimation is the primary cause of the former and entails an order of magnitude (or more) variability in cellular pigmentation over ecologically relevant light levels (e.g., Geider et al., 1985, 1986; Behrenfeld et al., 2002b).